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HABITAT USE BY SWAINSON'S WARBLERS IN A MANAGED BOTTOMLAND FOREST

SCOTT G. SOMERSHOE,[1,2,4] STEPHEN P. HUDMAN,[1,3] AND C. RAY CHANDLER[1]

ABSTRACT.—The Swainson's Warbler (*Limnothlypis swainsonii*) is a locally distributed and relatively uncommon Neotropical migrant songbird that breeds in the bottomland forests of the southeastern United States and spends the nonbreeding season in the Caribbean Basin. Populations of Swainson's Warblers have declined during recent decades as bottomland forests have come under increasingly intensive management and large areas have been converted to other land uses. We examined the habitat around song perches used by male Swainson's Warblers at Big Hammock Wildlife Management Area, a managed bottomland forest along the Altamaha River in Tattnall County, Georgia. We quantified 20 features of habitat structure in areas occupied by Swainson's Warblers (occupied plots) and two sets of controls: unoccupied plots adjacent to occupied plots (adjacent control plots) and unoccupied plots throughout the management area (general control plots). Occupied plots and adjacent control plots both differed in structure from the general control plots. We detected no significant differences, however, in vegetation structure between occupied plots and adjacent control plots. General control plots tended to have a greater number of trees, greater basal area, and a complete canopy, whereas occupied and adjacent control plots had high densities of small stems, cane, herbaceous ground cover, and leaf litter; this latter pattern is typical of documented Swainson's Warbler breeding habitat. Lack of significant differences in vegetation structure may be due to great variation in habitat structure around song perches, small sample size, or scarcity of Swainson's Warblers. Future research should focus on quantifying habitat characteristics around nest sites, song perches, and feeding areas. Our results suggest that management of bottomland habitats by thinning forests and encouraging regeneration of canebrakes is needed for successful conservation of Swainson's Warblers.
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The Swainson's Warbler (*Limnothlypis swainsonii*) is a locally distributed and relatively uncommon Neotropical migrant songbird that breeds in bottomland forests of the southeastern United States and spends the nonbreeding season in the Caribbean Basin (Meanley 1971, Brown and Dickson 1994). Populations of the Swainson's Warbler were suspected to be declining as early as 1971 (Meanley 1971), and a recent study indicated that the northernmost breeding populations in Maryland, Delaware, Missouri, and Illinois have disappeared during the last 30 years (Graves 2001). There is uncertainty about the status of Swainson's Warbler populations because standardized surveys (e.g., the Breeding Bird Survey) do not adequately sample Swainson's Warbler habitat. Thus, no strong correlations can be drawn about regional population trends. Nevertheless, greater numbers of Swainson's Warblers have been detected where they persist, but many local populations have become extirpated (Graves 2001).

Swainson's Warbler population declines have been attributed to habitat loss on both the breeding and wintering grounds (Graves 2001). On the breeding grounds, development of bottomland forests for other land uses (e.g., agriculture, reservoirs, pine plantations, housing development) has forced Swainson's Warblers into smaller patches of potentially less suitable habitat, which may affect breeding success and long term population persistence. Factors such as loss of breeding and wintering habitat, low population densities, and lack of information about breeding biology have contributed to making this species a top conservation priority (Hunter et al. 1993, Smith et al. 1993, Thompson et al. 1993).

Understanding the factors that influence reproductive success of Swainson's Warblers, such as habitat associations, is essential to developing appropriate conservation strategies for this species. In the southeastern portion of their breeding range, Swainson's Warblers

[1] Dept. of Biology, Georgia Southern Univ., Statesboro, GA 30460-8042, USA.
[2] Current address: USGS Patuxent Wildlife Research Center, 2524 S. Frontage Rd., Vicksburg, MS 39180, USA.
[3] Current address: Dept. of Biology, Univ. of Vermont, Burlington, VT 05405, USA.
[4] Corresponding author; e-mail: scott_somershoe@usgs.gov

typically are associated with well-shaded forested floodplains that contain dense undergrowth, including thickets, giant cane (*Arundinaria gigantea*), and semi-aquatic vegetation (Brewster 1885, Meanley 1971) interspersed with areas of little or no herbaceous ground cover (Meanley 1966, Eddleman et al. 1980, Thomas et al. 1996), and an extensive carpet of leaf litter overlying moist soils (Graves 1998). Thus, a suitable mosaic composition of the forest understory is thought to be more important to attracting Swainson's Warblers than the presence of a canebrake (Brown and Dickson 1994; Graves 2001, 2002). Specifically, dense areas are used for nesting and more open areas are used primarily for singing and foraging (Brown and Dickson 1994).

Breeding habitat appropriate for Swainson's Warblers historically was abundant in the extensive bottomland forests of the southeastern United States (Brantley and Platt 2001). As these forests have experienced increasingly intensive management for other land uses, the quality and availability of habitat have been reduced greatly (Meanley 1971, U.S. Dept. of the Interior 1993, Brown and Dickson 1994, Graves 2001) and probable breeding populations of Swainson's Warblers have been found in atypical habitats. For example, Swainson's Warblers recently were discovered in old growth bottomland forest fragments (see review in Graves 2001), a sweet gum (*Liquidambar styraciflua*) forest with a continuous understory of Chinese privet (*Ligustrum sinense*; SGS unpubl. data), and pine plantations with a deciduous understory (D. Roome pers. comm.). As a result, a quantitative analysis of the habitat within Swainson's Warbler territories is needed from managed forests, which are becoming an increasingly common feature of the environment. Furthermore, a quantitative comparison of occupied habitat to that generally available in managed forests is important for developing conservation strategies for Swainson's Warblers. The objective of this study was to conduct a quantitative analysis of habitat used by territorial male Swainson's Warblers in comparison to habitat in adjacent unoccupied areas and habitat generally available in a managed bottomland forest.

STUDY AREA AND METHODS

We conducted this study at Big Hammock Wildlife Management Area (BHWMA), a 2,605-ha area located on the northern shore of the Altamaha River in Tattnall County, Georgia (31° 50′ N, 82° 02′ W). BHWMA consists primarily of managed second growth bottomland hardwood forest with adjacent upland forest of varying age and forest type. The bottomland forest canopy is dominated by oak (*Quercus* spp.), sweet gum, ash (*Fraxinus* spp.), bald cypress (*Taxodium distichum*), and elm (*Ulmus* spp.). The understory includes American hornbeam (*Carpinus caroliniana*), red maple (*Acer rubrum*), river birch (*Betula nigra*), hawthorn (*Crataegus* spp.), holly (*Ilex* spp.), green briar (*Smilax* spp.), blackberry (*Rubus* spp.), and cane.

We surveyed BHWMA during 15 h of observation on 10 days from 12 May to 16 July 1999 by driving slowly (about 5 km/h) along a predetermined route, which allowed for an audible survey of a large portion of the bottomland forest in the management area. On two survey days we also walked two trails leading into areas we could not survey by vehicle. We visually located each singing male Swainson's Warbler (n = 12) and mapped the location of singing and foraging perches. We relocated all birds within their territories on at least three different days. We captured all 12 males using mist nets and song playbacks and we marked each bird with a USFWS aluminum leg band.

We quantified habitat structure using 11.3-m radius (0.045-ha) plots following James and Shugart (1970). We centered a plot on sites where each banded male repeatedly had been observed visiting and singing, for a total of 12 occupied plots. Because 11 of the 12 individual males were detected within 0.6 km of the Altamaha River (along a 3.3-km continuous stretch), we randomly selected 11 unoccupied plots along the river corridor that were adjacent to (but >250 m from) plots occupied by Swainson's Warblers (adjacent control plots). We used our map of known territories to determine potential adjacent control locations and used a coin and random numbers table to determine the side of the road and the distance (20–100 m) from the road where the plot would be located. The 12th random plot was

TABLE 1. Mean percentage of stems and basal area of some tree species varied significantly among occupied Swainson's Warbler territories (n = 12), adjacent control plots (n = 12), and general control plots (n = 12). Data were collected in the Big Hammock Wildlife Management Area, Tattnall County, Georgia, 1999.

	Occupied			Adjacent control			General control			P[a]	
Tree species	Stems	Basal area	Plots (n)	Stems	Basal area	Plots (n)	Stems	Basal area	Plots (n)	Stems	Basal area
Sweet gum, *Liquidambar styraciflua*	30.6	25.7	10	33.4	25.0	10	16.9	18.4	10	0.22	0.695
Water oak, *Quercus nigra*	13.6	15.7	6	0.5	0.1	1	0.8	0.7	1	0.01	0.013
American hornbeam, *Carpinus caroliniana*	12.2	7.0	8	26.8	17.8	8	9.9	4.3	6	0.19	0.155
Other spp.	8.4[b]	13.4	6	18.2[c]	26.9	9	10.0[d]	10.0	9	0.18	0.302
Laurel oak, *Q. laurifolia*	8.4	11.8	4	6.1	11.7	4	17.7	23.3	8	0.17	0.188
Willow oak, *Q. phellos*	7.4	12.0	4	5.7	7.6	5	18.7	22.3	10	0.13	0.174
Elms, *Ulmus* spp.	7.3	7.0	6	6.7	6.5	6	5.2	3.4	8	0.95	0.766
Ashes, *Fraxinus* spp.	5.9	5.3	2	0.6	1.1	1	6.5	5.4	6	0.13	0.155
Dead stems	4.9	3.4	5	0.0	0.0	0	8.5	7.8	9	0.002	0.003
Red maple, *Acer rubrum*	1.4	0.5	1	1.9	3.2	2	5.6	4.3	4	0.15	0.152

[a] Kruskal-Wallis ANOVA; Bonferroni adjustment: $P > 0.005$ not significant (0.05/10 = 0.005).
[b] *Nyssa sylvatica, Pinus taeda, Q. michauxii, Q. alba.*
[c] *P. taeda, Q. alba, Celtis laevigata, Cornus alternifolia, Crataegus* spp., *Betula nigra, Melia azedarach.*
[d] *Q. alba, Q. michauxii, B. nigra, Crataegus* spp., *Taxodium distichum, Acer negundo.*

near the one Swainson's Warbler located away from the river and was selected in a manner similar to the other plots. In general, we paired adjacent control plots with occupied plots. In addition, to allow a comparison of the habitat used by Swainson's Warblers to that generally available within BHWMA, we randomly selected 12 more plots (general control plots) on a grid of the entire management area, such that general control plots were >250 m from occupied or adjacent control plots. We gathered habitat structure data from August through September, 1999.

We measured size (dbh) of all woody stems ≥10 cm (trees) and identified each to species. We further categorized trees into six size classes for analysis: 10–14.9 cm, 15–19.9 cm, 20–29.9 cm, 30–44.9 cm, 45–59.9 cm, and >60 cm. We calculated mean basal area for each tree species. We quantified the number of shrub stems (<10 cm) per species along four 11.3 × 1.5-m belt transects and calculated stem density within each plot. We estimated percent canopy and herbaceous cover at 21 points (at about 2-m intervals) within each plot (one at the center and five points along each transect). We took five measures of litter depth at the first 2-m interval along each of the four transects and used mean litter depth for each plot in our analyses.

We used Kruskal-Wallis tests to evaluate differences in vegetation characteristics among plots because parametric assumptions were not met. Probabilities were Bonferroni adjusted for the number of simultaneous tests. We transformed habitat structure data using principal components analysis (PCA) and we compared individual PC scores among plot types with Kruskal-Wallis ANOVA. We used an orthogonal planned contrast to compare habitat along the Altamaha River (occupied and adjacent control plots) to that generally available at BHWMA (general control plots). We used a second orthogonal planned contrast to compare occupied plots to adjacent control plots to detect potential structural differences between occupied and unoccupied habitat. We set $\alpha = 0.05$ for all tests, and we analyzed all data using JMP 3.02 statistical software (SAS Institute, Inc. 1995).

RESULTS

The most common tree species, sweet gum, was distributed evenly across the three plot categories (Table 1). General control plots contained more dead trees than occupied and adjacent control plots. Occupied plots had more water oak (*Quercus nigra*) than adjacent control and general control plots.

Kruskal-Wallis ANOVA did not reveal significant differences in vegetation structure across plot types (Table 2). We used 20 variables in a principal components analysis to compare habitat structure among occupied, adjacent control, and general control plots. PC1 described a habitat gradient of large numbers of trees, basal area, and a complete canopy to habitat with an extensive litter layer, large percent herbaceous ground cover (i.e., grasses), and large numbers of cane, sweet gum, and other small stems. The gradient described by PC2 ranged from a large basal area of hornbeam, and large amounts of small trees/ha and herbaceous ground cover to areas with large sweet gum basal area, small stems and *Ilex* stems/ha. PC3 depicted a trend of large laurel (*Q. laurifolia*) and water oak basal area and number of large trees/ha to plots of large willow oak basal area, 30.0–49.9-cm trees/ha, and a large density of hornbeam stems. Vegetation structure differed significantly among plot categories along the first principal component axis (PC1: $F_{2,35} = 5.49$, $P = 0.009$), but we detected no significant differences along PC2 ($F_{2,35} = 0.90$, $P = 0.41$) or PC3 ($F_{2,35} = 0.33$, $P = 0.73$; Table 2).

DISCUSSION

Habitat structure in occupied and adjacent control plots was significantly different from the habitat generally available (general control plots) at BHWMA. General control plots typically were characterized as mature, open forest with relatively large numbers of trees and a complete canopy, which were features not typically associated with Swainson's Warblers (Brown and Dickson 1994, Graves 2001). In contrast, occupied plots and adjacent control plots were characterized by high densities of cane and small stems, and abundant leaf litter and herbaceous ground cover, all of which were structural characteristics associated with Swainson's Warblers at other locales (Brown and Dickson 1994; Graves 1998, 2001), and there was no detectable difference between the two plot types.

Stand history and flooding frequency and duration may explain differences in habitat structure among plots, as characterized by PC1. Areas that had evidence of prolonged flooding (i.e., the general control plots) tended to have many large trees and few small stems, which is not considered favorable Swainson's Warbler habitat (Graves 2001). The thick understory that describes occupied and adjacent control plots was due to less frequent and/or extensive flooding and increased canopy gaps from tree falls, which increased light availability and allowed thickets of cane and small stems to thrive. Thus, increased disturbance from tree falls provides for the development of suitable habitat for Swainson's Warblers (Graves 2002).

We found general differences in tree species composition and abundance among plot types. Compared to adjacent control plots, Swainson's Warblers were found in sites with greater amounts of water oak and tended to avoid high densities of American hornbeam and willow oak. Selection of water oak was noted for Swainson's Warblers at a breeding site in Louisiana (D. Roome pers. comm.). Graves (2001, 2002), however, found that Swainson's Warblers did not show selective use of specific floristic characteristics throughout the core breeding range of the species. Differences in floristic values between the general control plots and the occupied and adjacent control plots may be due to differences in the local hydrological gradient, which influences tree species composition. In addition, floristic values also may be related to the local stand history as the loss of canopy trees, through thinning or tree falls, facilitate the invasion of understory species.

Although our results generally agree with other descriptions of Swainson's Warbler habitat, the mean cane density we observed (1,748 stems/ha) around song perches was lower than that reported at another location in Georgia (50,000 stems/ha; Meanley 1971) or in Illinois (5,000 stems/ha; Eddleman et al. 1980). Occupied plots contained fewer trees relative to unoccupied habitat, but our large percent canopy closure (range 70–100%) was similar to the 85–90% canopy closure reported by Eddleman et al. (1980). In contrast to Eddleman et al. (1980) and Thomas et al. (1996), occupied plots at BHWMA had relatively high herbaceous ground cover (range 55–90%). Differences between this study and the literature may indicate that the species uses a larger range of forested habitats than previously known.

Although we measured numerous pertinent habitat variables, we did not detect differences in habitat structure between occupied and adjacent control plots. One explanation is that

TABLE 2. Habitat variables measured in occupied Swainson's Warbler territories (n = 12), adjacent control plots (n = 12), and general control plots (n = 12) did not differ significantly in univariate analyses, but the first principal component generated by these variables did differ significantly among plots. Data were collected in Big Hammock Wildlife Management Area, Tattnall County, Georgia, during 1999.

	Mean values (range)		
Variable	Occupied	Adjacent control	General control
Basal area (m^2/ha)			
American hornbeam, *Carpinus caroliniana*	0.8 (0–2.6)	1.5 (0–3.3)	0.7 (0–3.1)
Sweet gum, *Liquidambar styraciflua*	3.9 (0–12.6)	2.5 (0–11.9)	3.1 (0–10.9)
Laurel oak, *Quercus laurifolia*	2.1 (0–12.3)	2.4 (0–20.3)	6.4 (0–25.7)
Water oak, *Q. nigra*	2.1 (0–10.3)	0.0 (0–0.4)	0.0 (0–0.6)
Willow oak, *Q. phellos*	0.8 (0–5.9)	1.1 (0–6.6)	4.3 (0–22.1)
Other tree spp.	3.9 (0–8.0)	4.5 (0–20.5)	8.6 (0–34.1)
Tree density (stems/ha)			
Sweet gum, *Liquidambar styraciflua*	100 (0–688)	120 (0–821)	102 (0–955)
Holly, *Ilex* spp.	111 (0–466)	50 (0–488)	89 (0–311)
American hornbeam, *Carpinus caroliniana*	242 (0–1776)	285 (0–1621)	165 (0–1088)
10.0–14.9 cm dbh	141 (44–378)	115 (0–200)	224 (67–422)
15.0–19.9 cm dbh	85 (0–156)	80 (0–133)	117 (22–311)
20.0–29.9 cm dbh	74 (0–222)	39 (0–89)	109 (22–200)
30.0–44.9 cm dbh	44 (0–156)	28 (0–111)	61 (0–156)
45.0–59.9 cm dbh	6 (0–22)	11 (0–44)	11 (0–22)
>60 cm dbh	4 (0–22)	6 (0–44)	6 (0–44)
Other stem density (stems/ha)			
Shrubs	606 (44–1576)	865 (178–2730)	314 (66–710)
Cane, *Arundinaria* spp.	1748 (0–7747)	601 (0–2819)	163 (0–1443)
Percent cover			
Canopy	0.9 (0.7–1)	0.8 (0.4–1)	0.9 (0.6–1)
Herbaceous ground	0.6 (0.6–0.9)	0.6 (0.5–0.8)	0.5 (0.1–0.9)
Mean litter depth (cm)	1.9 (0.5–2.8)	2.3 (0.3–4.3)	1.3 (0.8–2.8)
Eigenvalue			
Percent variation explained			
Cumulative variation explained			

the mosaic of habitats that are utilized within territories may have produced too much variation in the data for relatively small differences to be detected (Brown and Dickson 1994; Graves 2001, 2002). Furthermore, our small sample size may have reduced our power for detecting structural differences between occupied and adjacent control plots. Alternatively, we suggest that at BHWMA there may be unoccupied sites suitable for territories. Although the density of Swainson's Warblers at our study area was comparable to that reported by Meanley (1971) from another locale in Georgia, there may not be enough Swainson's Warblers to fill the remaining unoccupied habitat.

In summary, our study quantified structural characteristics of Swainson's Warbler song perches and provides a general assessment of occupied habitat in a managed bottomland forest landscape in southeastern Georgia. Although our sample sizes were small, Swainson's Warbler habitat use seems to be highly specific. To better understand the habitat requirements of Swainson's Warblers, future research should focus on quantifying habitat structure around nesting sites, song perches, and other areas within territories. Furthermore, efforts should be directed at a comparative approach of estimating habitat use, territory size, and nest success in typical and atypical Swainson's Warbler habitats.

Nevertheless, if Swainson's Warbler is a conservation priority in the southeastern United States, we then suggest providing a combination of both dense canebrakes and open

TABLE 2. Extended.

Kruskal-Wallis ANOVA		Principal components factor loadings		
χ^2	P^a	PC1	PC2	PC3
2.4	0.294	0.0082	0.5257	−0.1343
0.6	0.754	0.0371	−0.3186	−0.0913
4.6	0.102	0.3294	−0.1722	0.3059
8.9	0.011	0.3294	−0.1722	0.3059
5.3	0.072	0.1119	−0.1521	−0.2383
3.2	0.055	0.2343	0.1869	−0.0808
2.7	0.253	−0.2848	−0.2658	−0.0088
4.5	0.105	0.0513	−0.2694	−0.1382
1.8	0.399	−0.1595	0.0951	−0.3717
5.9	0.052	0.2338	−0.0634	−0.0431
0.4	0.824	0.2557	0.2566	−0.1159
9.2	0.099	0.3141	0.0035	−0.1928
2.5	0.284	0.2247	−0.0068	−0.3082
1.6	0.455	0.1628	0.1036	0.2557
0.0	0.995	0.0969	0.1227	0.5165
5.4	0.068	−0.2848	0.0066	0.1645
9.9	0.007	−0.2026	0.1198	0.1083
4.6	0.101	0.2607	0.0518	0.0349
2.9	0.225	−0.2515	0.3013	0.2119
6.4	0.042	−0.2474	−0.1361	0.0353
		5.42	2.19	2.04
		27	11	10
		27	38	48

[a] Bonferroni adjustment: $P > 0.0025$ not significant ($0.05/20 = 0.0025$).

understory habitats for attracting breeding birds. Regenerating canebrakes through removing some large trees, while providing a minimum of 70% canopy closure after thinning, and planting cane may facilitate canebrake regeneration and may provide an important step in producing potentially suitable habitat for Swainson's Warblers (Eddleman et al. 1980, N. Klaus pers. comm.). Analysis of flooding regime and stand history (i.e., time since thinning, species of trees removed during thinning, tree falls) may provide insight into current and future canopy and understory composition and ultimately the production of potential Swainson's Warbler habitat. In addition, establishing a canebrake monitoring system would provide information about the presence of Swainson's Warblers across years (Eddleman et al. 1980). Ultimately, regenerating canebrakes in bottomland forests and monitoring nesting success in established and regenerated canebrakes is critical to understanding population dynamics of the Swainson's Warbler in the southeastern United States.

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